

TSE M1 – Semester 1

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# Evolution of Economic Behavior

## Week 8:

Assortative matching, Hamilton's Rule  
and the evolution of cooperation



# Assortative matching, Hamilton's rule and the evolution of cooperation: outline

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- What does altruism mean to biologists, and why is it necessary for explaining cooperation?
- How assortative matching makes the evolution of biological altruism possible
- Some possible reasons for assortative matching
- Kin selection – how does it work?
- Special examples – social insects, cooperative breeding in birds

# What does altruism mean to biologists, and why is it necessary for explaining cooperation?

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- Altruism to biologists is not an emotion or other psychological concept – it's any behavior raising fitness of another individual at a cost to fitness of the individual engaging in the behavior
- Fitness – number of descendants in future generations
  - Rarely measured by next generation (quantity-quality)
  - Can be measured by number of grandchildren
- Much cooperative behavior raises an individual's fitness and needs no altruism to explain it

# How assortative matching makes the evolution of biological altruism possible (I)

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- Key lies in extending the notion of fitness to *inclusive* fitness
- What matters in explaining natural selection is not fitness of individuals – individuals are not the subject of natural selection
- It is the fitness of particular alleles of genes that determine traits....and genes do not have descendants, they have *copies*
- An individual's genes can have copies in other ways than by leading the individual to leave descendants
- They can lead *other* individuals to have descendants bearing copies of the genes

# How assortative matching makes the evolution of biological altruism possible (II)

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- Consider a population of individuals with a distribution of genotypes that is in steady-state equilibrium
- This means that, for every gene, all alleles present have the same fitness (otherwise the proportion of alleles in the population would be changing)
- Now consider a mutation – a new allele inclining the individual to behave more altruistically in a setting with Prisoners Dilemma payoffs, and individual fitness strictly increasing in payoffs
- The mutation will leave fewer copies of itself in that individual's descendants – is that enough to drive it out of the population?

# How assortative matching makes the evolution of biological altruism possible (III)

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- No! If the behavior is more likely to benefit other individuals bearing copies of the allele, these benefits can offset the cost to the individual herself
- If the allele has just mutated in the genotype of the bearer, there will be no other individuals bearing copies
- But if it mutated previously there may be other individuals bearing it in the population
- Assortative matching occurs if the bearer of the mutant gene is more likely to interact with (and thus benefit) another bearer of the gene than would be predicted from its population frequency

# Some possible reasons for assortative matching

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- Exogenous (eg geographical) mechanisms
- Multi-level selection
  - Note that this is not equivalent to altruism being selected “for the good of the species”
- Mutual recognition (“green beards”)
- Kin selection
  - Note that kin selection can interact with geographical mechanisms – via limited dispersal of offspring

# Kin selection: how does it work? (I)

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- Hamilton's rule: a gene favoring altruistic behavior is selected if

$$c < r B$$

- where  $c$  is fitness cost to bearer,  $B$  is fitness benefit to the other individual, and  $r$  is “coefficient of relatedness” between them
- This is sometimes misleading described as “the proportion of shared genes between the individuals”
- To see why this is misleading note that chimps and humans share over 98% of their genes



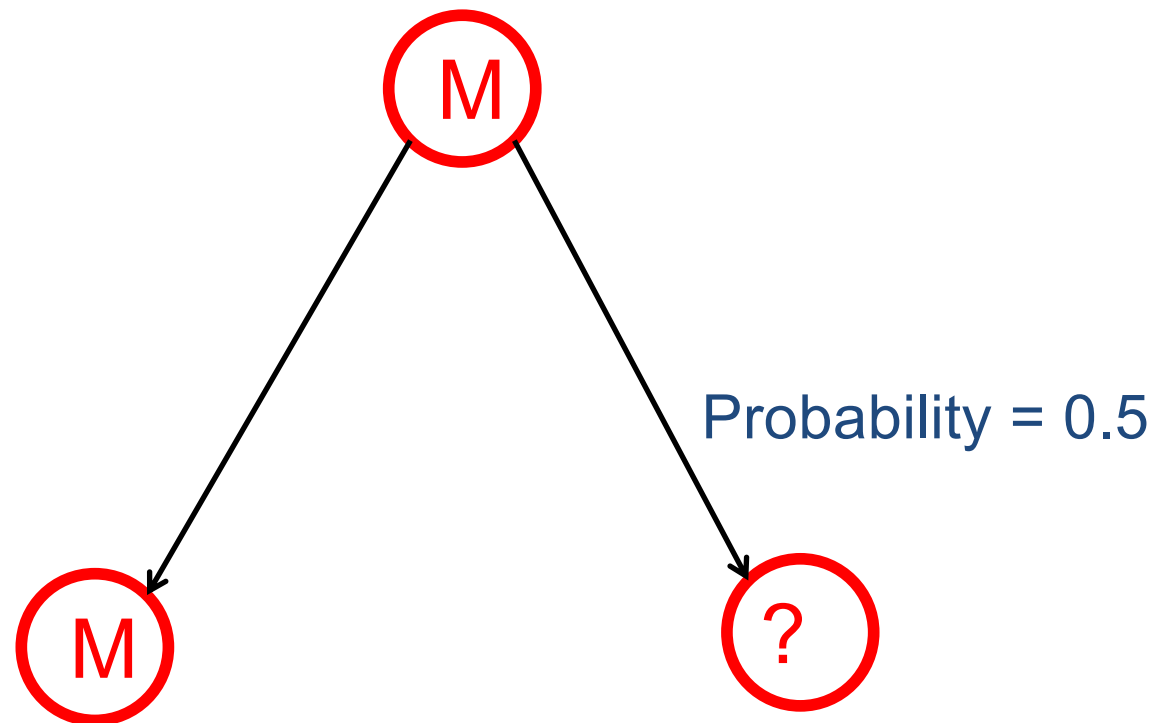
## Kin selection: how does it work? (II)

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- Coefficient of relatedness describes the probability that one individual will share a mutant allele that is borne by the other and also by their most recent common ancestor, and is otherwise present at a negligible frequency in the population
- Siblings have a 50% coefficient of relatedness because the common ancestor has a 50% probability of having passed the mutant allele on to the other sibling

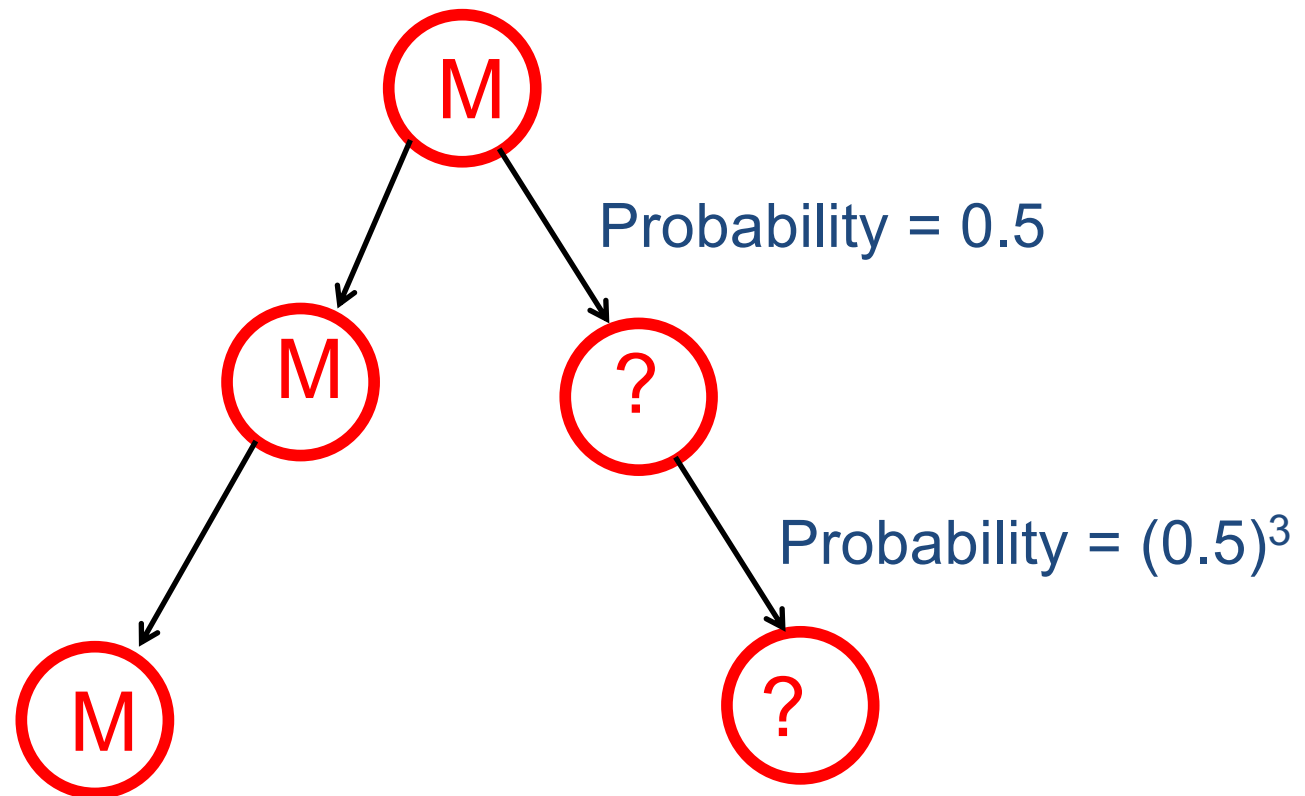
# Siblings

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# First cousins

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# Special examples

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- Eusocial insects (those with a sterile caste)
  - Some bees, wasps, almost all ants and all termites
  - Has some association with haplodiploidy: males develop from unfertilized eggs, females from fertilized ones (so males have a 100% coefficient of relatedness with daughters, and sisters 75% with each other).
  - Some mammals are eusocial (naked mole rats)
- Cooperative breeding in birds and some mammals (meerkats)